

RESPONSE OF THE BENTHIC MACROINVERTEBRATE COMMUNITY IN A NORTHERN MICHIGAN STREAM TO REDUCED SUMMER STREAMFLOWS

TODD C. WILLS,^{a*} EDWARD A. BAKER,^b ANDREW J. NUHFER^a and TROY G. ZORN^b

^a Michigan Department of Natural Resources, Hunt Creek Fisheries Research Station, 1581 Halberg Road, Lewiston, MI 49756, USA

^b Michigan Department of Natural Resources, Marquette Fisheries Research Station, 488 Cherry Creek Road, Marquette, MI 49855, USA

ABSTRACT

We evaluated the response of benthic macroinvertebrates in a Michigan trout stream to flow reduction by diverting water from a 602 m reach of Hunt Creek from June through August of 1994, 1997 and 1998. We also assessed the utility of the Physical Habitat Simulation system (PHABSIM) in predicting the response of benthic insects to water withdrawals by testing the assumption of a positive linear relationship between modelled habitat (weighted usable area, WUA) and the density of 13 benthic insect families. Our findings showed that the density of filter feeding and grazing insect taxa, as well as insects classified as obligate erosional zone taxa, declined significantly in the dewatered (treatment) zone (TZ) when 90% of flow was diverted. Density of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa in the TZ was significantly lower when 90% of water was diverted as compared to density at baseflow or when flow was reduced by 50%. The density of all insects in an upstream reference zone riffle (RZ), where flow was not altered, did not change among experimental periods. Although overall reductions in the density of benthic insects at 90% flow reduction coincided with lower PHABSIM predictions of WUA, we found poor linear correlation between WUA at different flows and the density of the 13 benthic insect families for which WUA was modelled. The low proportion of variation explained by WUA for all families modelled suggests that WUA alone is not an accurate predictor of benthic insect density. Resource managers should consider the potential consequences of water withdrawals to all components of stream communities, including benthic macroinvertebrates. However, caution should be applied when using the PHABSIM technique in groundwater-fed streams such as Hunt Creek, because most relationships between WUA and benthic insect density were insignificant. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: benthic macroinvertebrates; groundwater streams; flow reduction; PHABSIM

INTRODUCTION

Increasing water withdrawals for agricultural, industrial and domestic purposes in Michigan may adversely affect stream communities. The area of land irrigated for agricultural purposes in Michigan increased from 39 255 ha to 159 042 ha statewide between 1974 and 1997 (USDA, 1999). Seasonal withdrawals to irrigate golf courses accounted for an additional 15 378 ha of land in Michigan in 1999 (Michigan Water Use Reporting Program, unpublished data). Such increases in water use are a potential threat to streams and raise concerns about the effects of water withdrawals on all components of Michigan's stream communities, including benthic macroinvertebrates.

Benthic macroinvertebrates are an important food source for fishes, including ecologically and economically significant salmonid species (Elliott, 1973; Alexander and Gowing, 1976; Allan, 1981; Bechara *et al.*, 1992; Nielsen, 1992). Macroinvertebrates are also crucial to nutrient cycling and energy flow through lotic systems (Rader and Belish, 1999). For example, Chapman (1966) noted that the density of macroinvertebrates and their occurrence in the drift has the potential to limit the growth rate of individual fish and the size of the population. Rader and Belish (1999) noted that there is a wealth of literature suggesting that macroinvertebrate communities are

*Correspondence to: T. C. Wills, Michigan Department of Natural Resources, Hunt Creek Fisheries Research Station, 1581 Halberg Road, Lewiston, MI 49756, USA. E-mail: willst@michigan.gov

Contract/grant sponsor: Federal Aid in Sport Fish Restoration Act; contract/grant number: 736, Project F-80-R, Michigan.
Contract/grant sponsor: MDNR Fisheries Division

Received 18 April 2005
Revised 15 December 2005
Accepted 1 February 2006

tightly linked to instream hydraulic conditions such as flow variation. Although numerous studies have examined the effects of increased flow conditions on macroinvertebrates (Boulton and Lake, 1992; Cobb *et al.*, 1992; Imbert and Perry, 2000), few reports exist on the effects of dewatering (reducing flow) on invertebrates. Studies that have examined the effects of dewatering on macroinvertebrates have primarily been undertaken in other countries (O'Keefe and DeMoor, 1988; Dudgeon, 1992; Castella *et al.*, 1995), or in streams in the western United States not comparable to groundwater-fed streams found in Michigan (e.g., McClay, 1968; Minshall and Winger, 1968; Rader and Belish, 1999).

Concerns about the effects of excessive water withdrawals on stream communities in the western United States led to the development of the Instream Flow Incremental Methodology (IFIM), a protocol for protecting stream flows that is dependent upon field data collection, habitat modelling and negotiation over the projected effects of reduced streamflow on fish and aquatic habitat (Milhous *et al.*, 1989). Although the IFIM, including its suite of habitat modelling programmes collectively known as the Physical Habitat Simulation system (PHABSIM), has been widely applied in the western United States, the system has not been extensively used in Michigan to evaluate the effects of water withdrawals (Gowan, 1984; Reiser *et al.*, 1989; Bovee *et al.*, 1994; Baker and Coon, 1995a, 1995b; Nuhfer and Baker, 2004).

Baker and Coon (1995b) developed habitat suitability criteria (HSC) from benthic macroinvertebrate samples collected from Hunt Creek, Michigan and used PHABSIM to predict habitat availability for major taxa at different levels of stream discharge. They predicted that a water withdrawal of 50% would reduce habitat of riffle dwelling taxa, such as Heptageniidae, but would have little effect on most other taxa examined. Heptageniidae density in a treatment riffle (50% flow reduction) did decrease significantly in relation to a control riffle. However, there were no significant changes in either total density of benthic macroinvertebrates or density of other taxa examined ($N = 13$). Several other studies have documented habitat use patterns of benthic macroinvertebrates and have published HSC which could be used in a PHABSIM analysis (e.g. Gore and Judy, 1981; Orth and Maughan, 1983; Gore, 1989), but the availability of these data has not led to an increase in the use of benthic macroinvertebrates to predict the effects of flow alteration in streams (Baker and Coon, 1995b; Gore, *et al.*, 2001). Bovee (1985) studied the effects of a peaking hydropower operation on benthic macroinvertebrate habitat in a Colorado stream but did not relate the weighted useable area (WUA) projections from the PHABSIM modelling to observed benthic macroinvertebrate abundance. Likewise, Gowan (1984) modelled the habitat of two genera of macroinvertebrates in a marginal Michigan trout stream, but did not compare the PHABSIM model output with observed macroinvertebrate densities. Although several authors (Mathur *et al.*, 1985; Morhardt, 1986) and nationwide surveys of IFIM users in the United States (Reiser *et al.*, 1989; Armour and Taylor, 1991) have indicated that one of the areas of the IFIM most in need of research concerns the assumption of a positive linear relationship between WUA and fish biomass (Zorn and Seelbach, 1995), we are unaware of any studies that have attempted to determine if a positive linear relationship exists between WUA and benthic macroinvertebrate abundance.

The objectives of this study were to (1) evaluate the response of the benthic macroinvertebrate community in Hunt Creek to simulated irrigation withdrawals by determining the effects of dewatering on benthic macroinvertebrate density, and (2) determine if densities of select benthic insect families were correlated with PHABSIM projections of WUA at different discharge levels.

METHODS

Study stream

Hunt Creek is a groundwater-fed tributary to the Thunder Bay River in Michigan's northern Lower Peninsula (Figure 1). The Hunt Creek watershed lies in northern Oscoda and southern Montmorency counties and drains extensive glacial sands and gravels deposited approximately 10 000 years ago (Dorr and Eschman, 1970). Due to the geology of the watershed, Hunt Creek has extremely stable discharge: at the downstream end of the study area the 90% exceedence flow was 0.75 m³/s and the 10% exceedence flow was 0.87 m³/s from 15 March 1999 to 15 March 2001 (Nuhfer and Baker, 2004). Hunt Creek is a second-order stream upstream of the confluence with Fuller Creek, which flows into Hunt Creek immediately above the treatment zone (Figure 1), and is a third-order

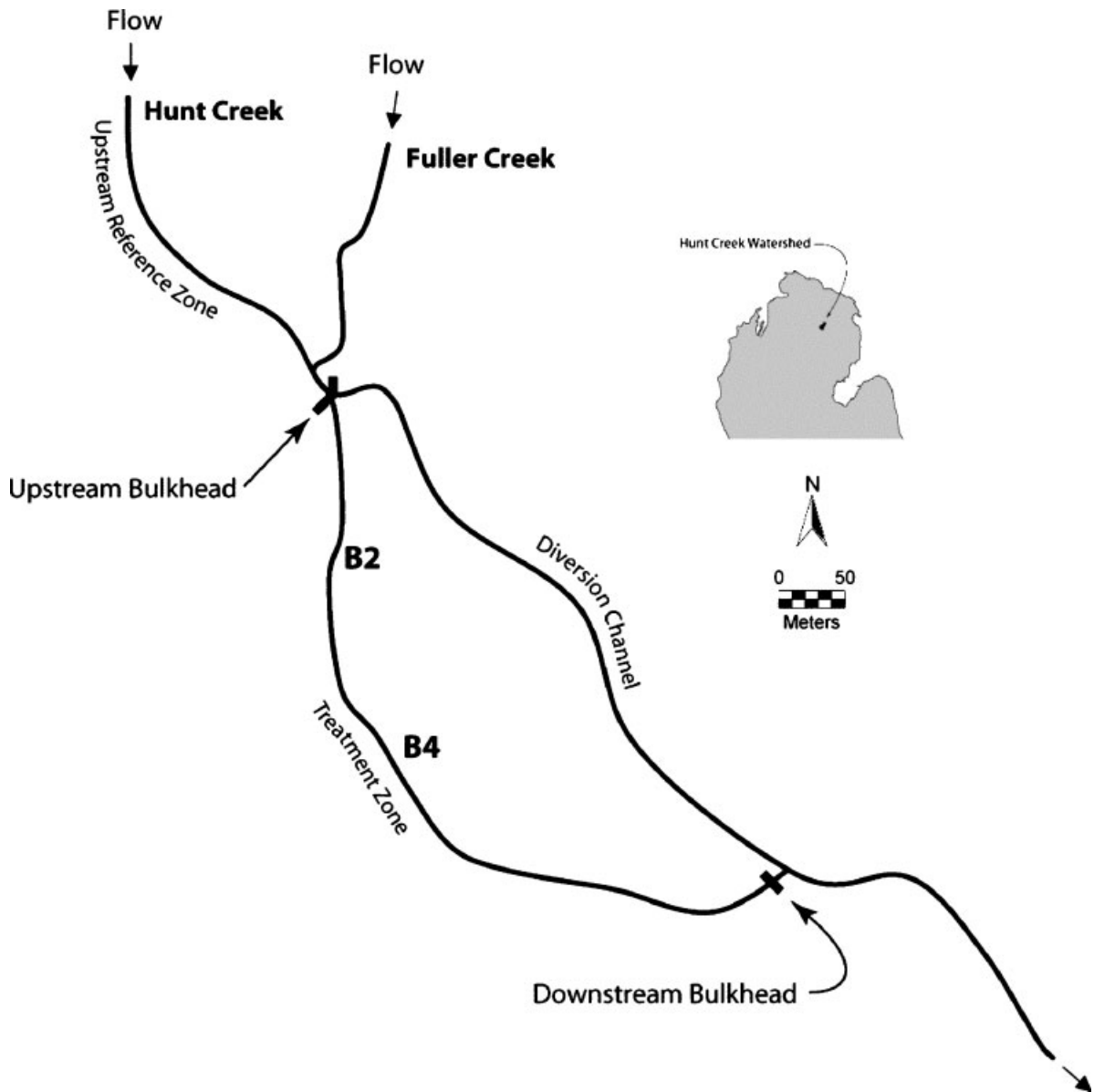


Figure 1. Map of the Hunt Creek study area. The upstream bulkhead was the boundary between the upstream reference zone and the treatment zone. Inset shows the position of the Hunt Creek watershed in the northeastern portion of Michigan's Lower Peninsula

stream through the remainder of the study area. Common fish species in Hunt Creek include brook trout *Salvelinus fontinalis*, mottled sculpin *Cottus bairdi*, and slimy sculpin *Cottus cognatus* (Alexander and Hansen, 1986).

Water diversions

To determine species-specific habitat-discharge suitability relationships and test PHABSIM, Nuhfer and Baker (2004) divided a study area of Hunt Creek into three contiguous sections: a 1254-m upstream reference zone (RZ), a 602-m treatment zone (TZ, Figure 1), and a 1534-m downstream RZ. In 1989–90, a diversion channel was excavated around the TZ. Bulkheads were installed at the upstream and downstream ends of the TZ as a means of controlling discharge and to support traps used in monitoring fish movement. The upstream bulkhead diverted

water around the TZ (simulating irrigation withdrawals) from 1 June to 31 August of each year in 1991–98. During 1991–94, 50% of the streamflow was diverted from the TZ, followed by a 75% diversion of streamflow in 1995–96 and a 90% diversion of streamflow in 1997–98. Nuhfer and Baker (2004) did not randomly assign flow diversions to years due to concerns regarding the potential impacts of large streamflow diversions (e.g. 90%) on subsequent years with smaller streamflow diversions.

Construction of HSC

Macroinvertebrate abundance and habitat data were collected by Baker and Coon (1995b). Prior to sampling macroinvertebrates and macroinvertebrate habitat, they divided the TZ into seven contiguous reaches, each approximately 50 m in length, and omitted the small area of impounded water at the downstream end of the TZ and the disturbed habitat at the upstream end of the TZ immediately below the bulkhead.

Baker and Coon (1995b) collected benthic macroinvertebrates and depth, velocity and substrate data from randomly selected locations in the TZ during May–September, 1992 and April–September, 1993 to construct HSC. They constructed HSC for macroinvertebrate families from these combined TZ data using the nonparametric tolerance limits method described in Bovee (1986). Due to concerns regarding statistical independence of the observations, they did not weigh the value of the habitat measured at a sample location by the number of organisms in the sample, which resulted in HSC constructed from presence–absence data only. They also did not correct the HSC based on habitat availability because sample sites were randomly selected and therefore sampled in approximate proportion to their availability.

PHABSIM modelling

Baker and Coon (1995b) used a representative reach approach for modelling the habitat in the TZ by selecting two of the 50-m reaches in the TZ (reaches B2 and B4, Figure 1) for PHABSIM analysis. They established transect locations in each of the reaches and used changes in mesohabitat (riffle, run, pool) within each reach to guide transect placement. Depth, velocity and substrate data were collected along each transect at three discharges: $0.46 \text{ m}^3/\text{s}$ (0% flow reduction), $0.23 \text{ m}^3/\text{s}$ (50% flow reduction), and $0.11 \text{ m}^3/\text{s}$ (75% flow reduction). Baker and Coon (1995b) used PHABSIM to make projections of WUA for selected benthic insect families over a range of flows from summer baseflow down to 2% of summer baseflow ($0.01 \text{ m}^3/\text{s}$) for the reaches in the TZ. They selected families for PHABSIM modelling based on their frequency of occurrence in the 1992–93 samples and their habitat use characteristics (e.g. erosional vs. depositional areas). Habitat (WUA) was modelled for insect families that occurred in 20–80% of the samples in 1992–93, as well as additional families (Table I) to provide data for habitat types that were not adequately represented in the initial selection procedure.

Macroinvertebrate abundance

Macroinvertebrate abundance data were collected at 50% flow reduction in 1994 (Baker and Coon, 1995b) and at 90% flow reduction in 1997 and 1998. Macroinvertebrate collection and enumeration procedures for 1997–98 followed the protocols for 1994 detailed in Baker and Coon (1995b). Because early results of the PHABSIM modelling by Baker and Coon (1995b) indicated that riffle-dwelling insects were more likely to be affected by flow reductions than insects more commonly found in pool or depositional habitats, two riffles were selected (one each in the TZ and upstream RZ; hereafter referred to as the RZ) that had similar microhabitat characteristics under baseflow conditions in 1994. The microhabitat characteristics (depth, mean column velocity and substrate) of the riffles selected in the TZ and RZ were very similar to those found in the riffle habitat in reach B2 (Figure 1). They measured the width and length of each of the selected riffles and using permanent markers in the stream bank, established a two-dimensional grid of cells, each cell being approximately the same size as the area sampled by a Hess sampler (0.023 m^2). Benthic macroinvertebrate samples were collected in seven randomly selected cells in each riffle at approximately three week intervals from April or May to August during 1994, 1997 and 1998.

We moved upstream through each riffle and collected samples from each of the randomly selected cells with a modified Hess sampler constructed of 500- μm mesh. Upon collection, benthic samples were preserved in 95% ethyl alcohol and returned to the laboratory for processing. Macroinvertebrates were separated from inorganic

Table I. Percent frequency of occurrence of invertebrate taxa in samples collected from a treatment (dewatered) zone and reference zone of Hunt Creek in April through August of 1994, 1997 and 1998. Taxa selected for habitat modelling are in bold face type

Class	Order	Family	% occurrence			
			1994 (N = 83)	1997 (N = 70)	1998 (N = 68)	
Insecta	Coleoptera	Dytiscidae	0	1	2	
		Elmidae adult	84	40	35	
		Elmidae larvae	99	86	81	
		Undetermined	1	0	0	
	Diptera	Athericidae	11	0	4	
		Ceratopogonidae	6	3	25	
		Chironomidae	87	99	96	
		Empididae	69	21	35	
		Muscidae	1	0	0	
		Ptychopteridae	0	0	2	
		Simuliidae	52	11	24	
		Tabanidae	2	6	0	
		Tipulidae	4	16	9	
		Undetermined	46	1	0	
		Ephemeroptera	Baetidae	98	83	91
			Ephemerellidae	53	56	52
	Heptageniidae		83	43	63	
	Leptophlebiidae		2	0	4	
	Undetermined		0	3	0	
	Heteroptera	Gerridae	0	1	0	
		Hydrometridae	0	1	0	
	Megaloptera	Corydalidae	11	13	12	
		Sialidae	0	1	0	
	Odonata	Cordulegasteridae	1	0	0	
		Gomphidae	0	0	2	
	Plecoptera	Leuctridae	27	4	10	
		Nemouridae	70	37	35	
		Perlodidae	33	34	31	
		Undetermined	0	29	0	
	Trichoptera	Brachycentridae	15	27	21	
		Glossosomatidae	90	31	50	
		Goeridae	0	21	10	
		Hydropsychidae	47	21	13	
		Hydroptilidae	5	4	12	
		Lepidostomatidae	0	3	6	
		Limnephilidae	34	9	3	
		Philopotamidae	21	9	9	
		Rhyacophilidae	53	24	47	
		Uenoidae	0	34	52	
		Undetermined	59	26	0	
		Arachnida	Acari	Hydrocarina	16	40
Bivalvia		Pelecypoda	Sphaeriidae	0	4	2
	Unionoida	Unionidae	0	3	2	
	Undetermined	Undetermined	0	1	2	
Gastropoda	Bassomatophora	Physidae	0	3	6	
Hirudinea	Undetermined	Undetermined	1	0	0	
Malacostraca	Amphipoda	Gammaridae	98	90	94	
	Isopoda	Asselidae	15	17	27	
Oligochaeta	Lumbriculida	Lumbriculidae	0	9	13	
	Undetermined	Undetermined	100	89	85	
Turbellaria	Tricladida	Undetermined	1	1	4	

material in the samples by floating sample contents in a saturated sugar solution (Anderson, 1959). All macroinvertebrates were identified to family using the keys in Hilsenhoff (1995), Merritt and Cummins (1996), and Pennak (1989). Laboratory personnel counted the number of organisms in the sample by family and converted them to density estimates by dividing by the sampled area (0.023 m²). Sample data were not adjusted for the efficiency of the sugar floating procedure because the process was very efficient (Baker and Coon, 1995b).

Statistical analysis

We used mixed-effect analysis of variance (ANOVA) to evaluate the response of the benthic macroinvertebrate community in Hunt Creek to simulated irrigation withdrawals by comparing macroinvertebrate density in the TZ and RZ across three levels of flow reduction. We treated taxon group, functional feeding group or habitat guild, stream section (TZ or RZ), and level of flow reduction (0%, 50% or 90%) as fixed effects and sampling date as a random effect. We assigned organisms to functional feeding group (filter feeder, grazer, predator or shredder) or habitat guild (obligate erosional, obligate depositional, and erosional/depositional generalists) using the ecological tables presented in Merritt and Cummins (1996). In cases where the level of taxonomic identification required to functionally classify benthic insect families was not achieved (i.e. Tipulidae and Ephemerellidae), we assigned a functional feeding group or habitat guild to that family using the classification of the genus that most commonly occurred in Hunt Creek during the years of study (T. C. Wills, MDNR, unpublished data). Data collected prior to 1 June of each year of sampling were used to represent baseflow (0% flow reduction) conditions. We used a one-way ANOVA and Tukey's Honestly Significant Difference (HSD) test to identify significant differences in macroinvertebrate density at different levels of dewatering in the TZ. The same method was used to compare density between experimental periods in the RZ where flow was not altered. The data were transformed to meet the distributional assumptions of the model when appropriate, and rejection criteria was set at $\alpha = 0.05$ for all analyses.

Densities of insect families selected for habitat modelling were regressed against WUA to determine if a significant linear relationship existed between insect density and WUA. Because the riffle sampled in the TZ was close to reach B2 and similar to the riffles in reach B2, we regressed predictions of WUA in reach B2 against insect densities collected from the riffle sampled in the TZ at 0%, 50% and 90% flow reductions. We used WUA projections from the PHABSIM model developed by Baker and Coon (1995b) at 91% reduction in baseflow (Table II) as a surrogate for WUA at 90% reduction in baseflow. Rejection criteria was again set at $\alpha = 0.05$ for all analyses. All data analysis was done with SPSS version 11.5 (SPSS 2002).

Table II. Relation between computed weighted usable area (WUA, m²/100 m) and discharge for 13 benthic macroinvertebrate families selected for habitat modelling in an experimentally dewatered treatment zone of Hunt Creek

Order	Family	Discharge (m ³ /s)						
		0.01	0.04	0.07	0.11	0.17	0.23	0.46
		% flow reduction						
		98	91	85	76	63	50	0
Coleoptera	Elmidae adult	3.4	16.6	35.5	65.0	111.0	141.3	147.3
Diptera	Ceratopogonidae	88.1	132.8	163.1	188.9	212.2	217.3	180.3
	Empididae	13.9	42.1	72.8	107.4	148.7	171.0	156.6
	Simuliidae	4.7	29.6	65.7	108.7	153.0	175.8	169.2
	Tipulidae	30.8	66.0	99.7	135.8	173.8	192.2	157.4
Ephemeroptera	Baetidae	24.8	60.0	91.3	123.1	160.7	180.5	160.0
	Ephemerellidae	26.2	64.5	96.9	127.8	162.8	180.6	155.8
	Heptageniidae	6.7	20.8	35.9	59.1	99.2	130.7	153.4
Plecoptera	Nemouridae	29.8	77.0	115.1	148.4	180.2	193.1	164.7
	Perlodidae	9.1	36.2	68.6	104.8	145.3	166.6	165.4
Trichoptera	Glossosomatidae	11.0	37.4	66.2	97.8	138.1	161.2	148.0
	Hydropsychidae	5.2	24.7	50.6	85.7	130.9	155.1	147.8
	Rhyacophilidae	7.4	17.8	33.7	62.3	109.1	140.0	146.5

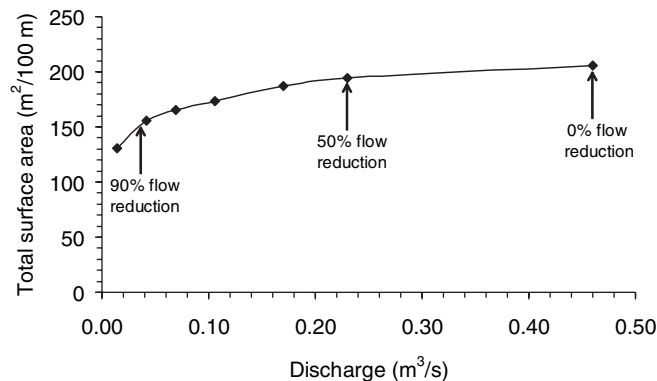


Figure 2. Total stream surface area ($\text{m}^2/100 \text{ m}$) as a function of discharge (m^3/s) for an experimentally dewatered treatment zone in Hunt Creek

RESULTS

PHABSIM model predictions of WUA

The results of HSC construction and PHABSIM modelling were summarized in Baker and Coon (1995b). The 50% reduction in summer stream flow in the TZ resulted in a minor loss of stream surface area (5.3%) in the modelled reach (B2), as total surface area decreased from 206 to $195 \text{ m}^2/100 \text{ m}$. Surface area was predicted to decline 29% in reach B2 when flow was reduced 90% (Figure 2).

Estimated WUA for a 50% reduction in flow was higher than at baseflow in reach B2 for all but three of the 13 taxa modelled (Elmidae adults, Heptageniidae, and Rhyacophilidae, Table II). The increases in WUA ranged from 0.7% for Perlodidae to 22.1% for Tipulidae. In general, taxa that were most commonly found in pool and depositional habitats had the largest increases in WUA (Figure 3). Elmidae adults, Heptageniidae, and Rhyacophilidae had minor losses in WUA (4.1–14.8%). Reducing baseflow by 90% resulted in a loss of WUA for all taxa modeled (Table II, Figure 3). Weighted useable area loss ranged from 26.3 to 88.7% (Ceratopogonidae and Elmidae adults, respectively). Weighted useable area estimates for more than half of the taxa modelled declined more than 70% (compared to baseflow) at a 90% reduction in summer stream flow (Table II).

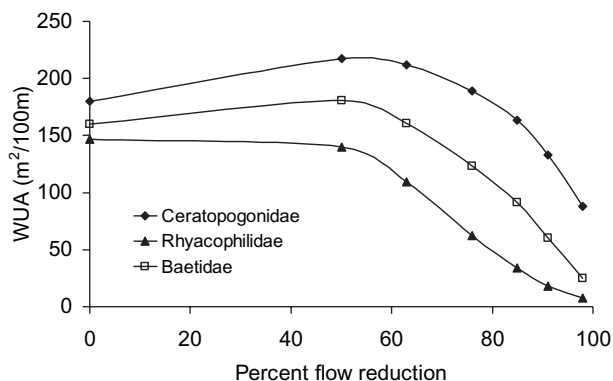


Figure 3. Relationship between weighted usable area (WUA, $\text{m}^2/100\text{m}$) and percent flow reduction for selected depositional (Ceratopogonidae), erosional (Rhyacophilidae), and erosional/depositional generalist (Baetidae) taxa in reach B2 in an experimentally dewatered treatment zone in Hunt Creek

Table III. *p*-values from mixed-effect analysis of variance modelling for the effects of stream section and level of flow reduction on benthic macroinvertebrate abundance

Metric	Source of variation	F	df	<i>p</i>
Total invertebrate abundance N = 32	Section	—	—	NS
	Flow	—	—	NS
	Section-flow	5.42	2, 13	0.019
Total insect abundance N = 32	Section	—	—	NS
	Flow	—	—	NS
	Section-flow	8.48	2, 13	0.004
Insect abundance by order N = 256	Order	512.09	7, 195	<0.001
	Section	9.23	1, 195	0.003
	Flow	—	—	NS
	Order-section	8.44	7, 195	<0.001
	Order-flow	5.01	14, 195	<0.001
	Section-flow	4.42	2, 195	0.013
	Order-section-flow	3.15	14, 195	<0.001
	Order-section-flow	3.15	14, 195	<0.001
EPT abundance N = 32	Section	—	—	NS
	Flow	6.84	2, 13	0.009
	Section-flow	11.43	2, 13	0.001

N refers to the total number of samples used in the analysis. EPT = Ephemeroptera, Plecoptera and Trichoptera taxa. NS = not significant

Effects of water withdrawal on benthic macroinvertebrate abundance

Total macroinvertebrate density. Benthic macroinvertebrates representing 7 classes, 16 orders, and over 40 families were present in a total of 221 samples collected during 1994, 1997 and 1998 (Table I). Macroinvertebrates from the class Insecta were most common and occurred in 100% of the samples, followed by classes Malacostraca (94.6%), Oligochaeta (54.8%), Arachnida (33.9%), Bivalvia (4.1%), Gastropoda (2.7%), Turbellaria (1.8%) and Hirudinea (0.5%).

The total density of benthic macroinvertebrates from all classes combined varied by stream section and level of flow reduction as indicated by the presence of a significant stream section-flow reduction interaction (Table III). Mean total density in the TZ was nearly 19% higher than the RZ at baseflow and over 40% higher than the RZ at 50% flow reduction ($t = 2.21$, $df = 13$, $p = 0.046$). At 90% flow reduction, mean total density was 41% lower in the TZ compared to the RZ ($t = 2.24$, $df = 13$, $p = 0.043$; Figure 4). Total invertebrate density significantly increased in the TZ when 50% of baseflow was diverted, but declined significantly when water diversions increased from 50 to 90% (Table IV).

Total insect density. Total insect density of all orders combined varied significantly by level of flow reduction, but the response differed between stream sections as indicated by the presence of a significant stream section-flow reduction interaction (Table III). Mean total insect density in the TZ was significantly higher than in the RZ at 50% flow reduction ($t = 3.04$, $df = 13$, $p = 0.010$; Figure 4). However, mean total insect density in the TZ was nearly 107% lower than in the RZ at 90% flow reduction ($t = 2.57$, $df = 13$, $p = 0.023$). Total insect density in the TZ declined significantly when flow was reduced by 90% whereas no change in density was observed in the RZ (Table IV, Figure 4).

Density of insects by order. The density of insects varied significantly by order and stream section (Table III). However, the presence of a significant order-stream section-flow reduction interaction complicates interpretation of the data, as insect density varied by order across both stream sections and all three levels of flow reduction (Figure 5). Relatively abundant insects from the orders Coleoptera and Trichoptera followed a pattern similar to mean total insect density, with greatest point estimates of mean density in the TZ occurring at 50% levels of flow reduction and very similar point estimates of mean density in the RZ across all levels of flow. Significant declines in the density of Coleoptera, Ephemeroptera and Trichoptera occurred when the percentage of water diverted from the TZ was increased from 50 to 90% (Table IV). Conversely, density of these taxa did not change in the RZ. No significant differences between the density of Plecoptera, Diptera or Megaloptera were detected in either zone. Benthic insects

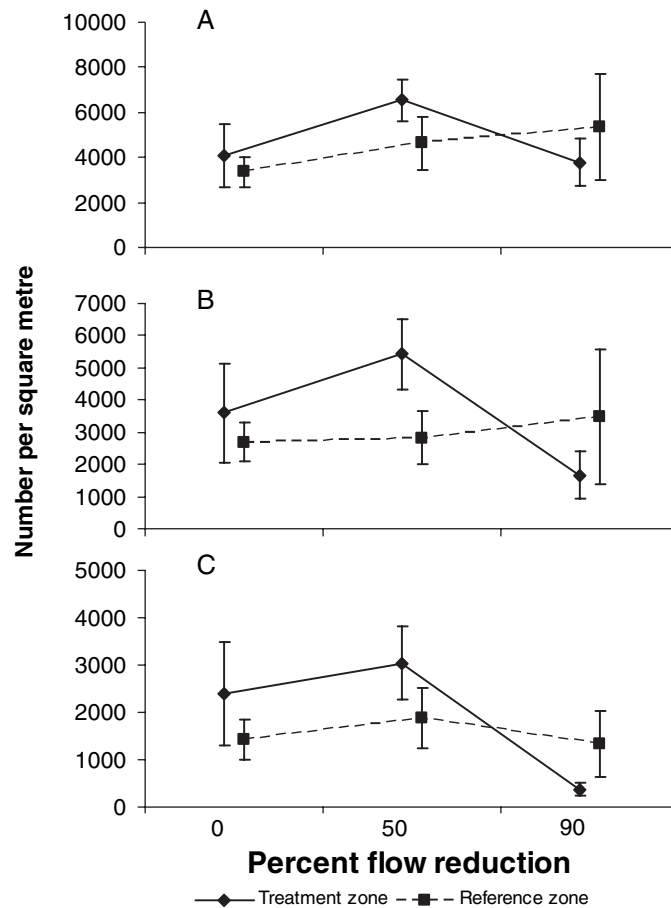


Figure 4. Mean number of invertebrates (A), insects (B), and Ephemeroptera, Plecoptera and Trichoptera taxa (C) per square metre (± 2 SE) in an experimentally dewatered treatment zone (TZ) and reference zone (RZ) in Hunt Creek. Summer discharge was reduced by 50% in 1994, and 90% in 1997 and 1998. Zero percent flow reduction represents summer discharge before water diversion was initiated in the TZ on June 1 of each year. Summer discharge in the RZ was not altered

from the orders Heteroptera and Odonata were uncommon in both stream sections across all levels of flow reduction.

The pattern of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa density also mirrored that of total insect density, as sensitive EPT taxa comprised a large proportion of the benthic insects sampled in both the TZ and the RZ (Table I). At baseflow, mean EPT density was significantly higher in the TZ compared to the RZ ($t = 2.94$, $df = 13$, $p = 0.011$). The mean density of EPT taxa in the TZ was higher compared to the mean density of EPT taxa in the RZ at 50% flow reduction ($t = 2.84$, $df = 13$, $p = 0.014$, Figure 4). At 90% flow reduction EPT taxa density in the TZ was lower than density in the RZ ($t = 2.87$, $df = 13$, $p = 0.013$). Density of EPT taxa in the TZ was significantly lower when 90% of water was diverted as compared to density at baseflow or when flow was reduced by 50% (Table IV, Figure 4).

Density of insects by functional groups. The density of insects varied significantly by functional feeding group regardless of stream section or level of flow reduction, and by level of flow reduction regardless of functional feeding group or stream section (Table V). However, the presence of significant stream section-flow reduction and functional group-stream section-level of flow reduction interactions indicated variability in the density of all insects between stream sections and among all levels of flow reduction. Density of grazers and filter-feeding taxa in the TZ declined significantly when 90% of water was diverted whereas no differences in density were evident in the RZ

Table IV. *p*-values from Tukey's Honestly Significant Difference (HSD) multiple comparison tests evaluating mean differences (number/m²) in the abundance of benthic macroinvertebrates among three levels of flow reduction in the treatment zone of Hunt Creek. No significant differences were found in the reference zone. N = 16 for all metrics. NS = not significant

Metric	Comparison (% flow reduction)	Mean difference	HSD (q = 3.73)	<i>p</i>
Total invertebrate abundance	50 vs. 0	2457.75	2347.82	0.040
	90 vs. 0	—	—	NS
	90 vs. 50	−2750.42	2347.82	0.022
Total insect abundance	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	−3745.92	2121.25	0.003
Insect abundance by order				
Coleoptera	50 vs. 0	1134.33	559.04	<0.001
	90 vs. 0	—	—	NS
	90 vs. 50	−1563.17	559.04	<0.001
Diptera	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Ephemeroptera	50 vs. 0	—	—	NS
	90 vs. 0	−1191.67	697.47	0.002
	90 vs. 50	−1227.00	779.79	0.003
Heteroptera	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Megaloptera	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Odonata	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Plecoptera	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Trichoptera	50 vs. 0	—	—	NS
	90 vs. 0	−808.33	0.43 ^a	0.002
	90 vs. 50	−1269.58	0.49 ^a	<0.001
EPT taxa abundance	50 vs. 0	—	—	NS
	90 vs. 0	−2015.50	1398.69	0.006
	90 vs. 50	−2662.00	1563.78	0.002

^aReflects HSD between log₁₀ transformed means used for statistical test.

(Table VI, Figure 6). No differences in the density of predators or shredders between treatment levels were detected in either zone.

Density of insects by habitat guilds. The density of insects varied significantly by habitat guild and stream section, but the response differed across levels of flow reduction as indicated by the presence of significant habitat guild-stream section, habitat guild-flow reduction, and stream section-flow reduction interactions (Table V). Average density of obligate erosional taxa in the TZ declined dramatically from 1 452/m² at 50% dewatering to 180/m² when 90% of water was diverted, whereas no change occurred in the RZ (Table VI, Figure 7). No change in the density of obligate depositional taxa was detected in either zone. The pattern of density for obligate depositional taxa in the TZ paralleled that of the RZ, with higher estimates of abundance in the TZ across all levels of flow. Generalist taxa that may occupy both erosional and depositional habitats were the most abundant insects encountered. Their density in the TZ increased significantly when 50% of baseflow was diverted, but declined significantly when water diversions increased from 50 to 90%. In the RZ, their density was similar between all periods (Table VI, Figure 7). Point estimates for taxa that use both habitat types were nearly identical at baseflow in

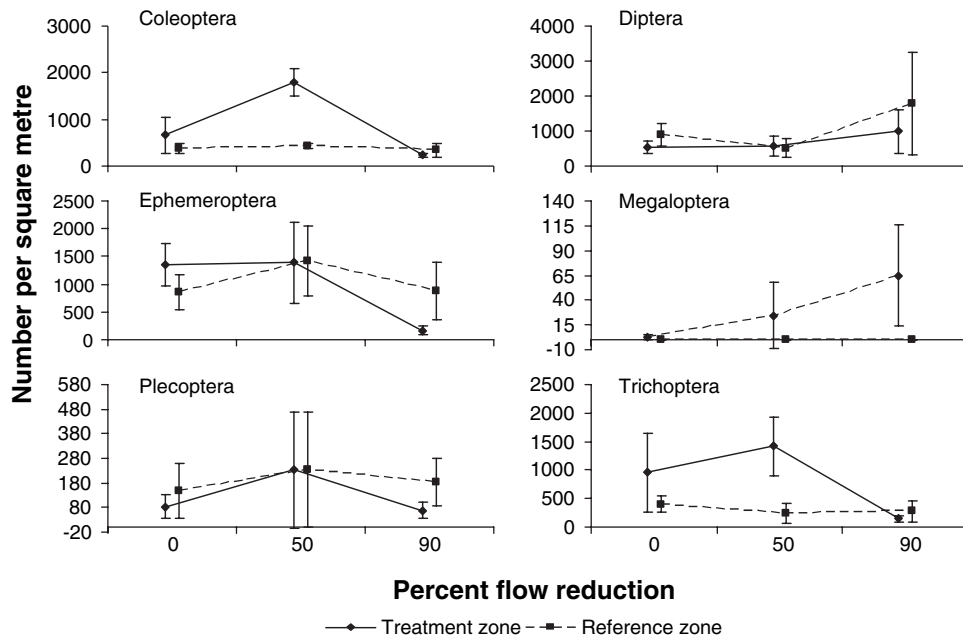


Figure 5. Mean number of insects per square metre (± 2 SE) for select orders in an experimentally dewatered treatment zone (TZ) and reference zone (RZ) in Hunt Creek. Summer discharge was reduced by 50% in 1994 and 90% in 1997 and 1998. Zero percent flow reduction represents summer discharge before water diversion was initiated in the TZ on June 1 of each year. Summer discharge in the RZ was not altered

the TZ and RZ. At 50% flow reduction, the point estimate of density was higher in the TZ compared to the RZ, and at 90% flow reduction the point estimate of density was lower in the TZ compared to the RZ.

Relationship of benthic insect abundance to WUA

The density of 3 of the 13 insect orders selected for PHABSIM modelling was significantly correlated to WUA estimates derived from presence-absence HSC (Table VII). The most significant relationship between density and

Table V. *p*-values from mixed-effect analysis of variance modelling the effects of stream section and level of flow reduction on the abundance of functional feeding groups (filter feeder, grazer, predator or shredder) and habitat guilds (obligate erosional, obligate depositional and erosional/depositional generalists). N refers to the total number of samples used in the analysis. NS = not significant

Metric	Source of variation	F	df	<i>p</i>
Abundance by functional group (<i>N</i> = 128)	Group	124.76	3, 91	<0.001
	Section	—	—	NS
	Flow	5.28	2, 13	0.021
	Group-section	—	—	NS
	Group-flow	2.73	6, 91	0.018
	Section-flow	11.04	2, 91	<0.001
	Group-section-flow	3.04	6, 91	0.009
Abundance by habitat guild (<i>N</i> = 96)	Guild	906.35	2, 65	<0.001
	Section	18.34	1, 65	<0.001
	Flow	—	—	NS
	Guild-section	13.14	2, 65	<0.001
	Guild-flow	21.12	4, 65	<0.001
	Section-flow	7.75	2, 65	0.001
	Guild-section-flow	—	—	NS

Table VI. *p*-values from Tukey's Honestly Significant Difference (HSD) multiple comparison tests evaluating mean differences (number/m²) in the abundance of functional feeding groups (filter feeder, grazer, predator or shredder) and habitat guilds (obligate erosional, obligate depositional, and erosional/depositional generalists) among three levels of flow reduction in the treatment zone of Hunt Creek. No significant differences were found in the reference zone. N = 16 for all metrics. NS = not significant

Metric	Comparison (% flow reduction)	Mean difference	HSD (q = 3.73)	<i>p</i>
Abundance by functional group				
Filter feeder	50 vs. 0	—	—	NS
	90 vs. 0	−170.33	0.81 ^a	0.003
	90 vs. 50	−519.33	0.90 ^a	<0.001
Grazer	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	−2612.83	2023.55	0.012
Predator	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Shredder	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Abundance by habitat guild				
Obligate erosional	50 vs. 0	—	—	NS
	90 vs. 0	−1573.00	963.99	0.002
	90 vs. 50	−1105.92	1077.78	0.044
Obligate depositional	50 vs. 0	—	—	NS
	90 vs. 0	—	—	NS
	90 vs. 50	—	—	NS
Erosional/depositional generalists	50 vs. 0	1924.92	1403.88	0.017
	90 vs. 0	—	—	NS
	90 vs. 50	−2292.42	1569.59	0.005

^aReflects HSD between log₁₀ transformed means used for statistical test.

WUA was for Heptageniidae (Figure 8). Although Heptageniidae density was positively related to WUA and the proportion of variation explained by WUA was moderate ($R^2 = 0.51$), there was considerable scatter around the linear regression line. The only other insect taxa for which density was significantly and positively related to WUA were Empididae and Baetidae. Evidence of a positive relationship between density and WUA was present for Glossosomatidae (Figure 8), as well as Ephemerellidae, Elmidae adults, Hydropsychidae and Nemouridae. However, scatter around the linear regression lines was considerable and the regression coefficients only approached significance, as the proportion of variation explained by WUA was small ($R^2 = 0.19$ – 0.26 , Table VII). The relationships between density and WUA for Ceratopogonidae, Perlodidae, Rhyacophilidae, Simuliidae and Tipulidae were insignificant.

DISCUSSION

Our results complement the results of previous studies. Total macroinvertebrate density and the total density of insect taxa (the most common benthic macroinvertebrates encountered in the field) were significantly higher in the TZ compared to the RZ when 50% of streamflow was diverted. McClay (1968) and Rader and Belish (1999) reported similar findings for insects in streams in the western United States when flow was reduced to 75% and 40% of baseflow, respectively. Both studies suggested several possible explanations, including the immigration of insects from dewatered areas. Although this could have occurred in our study, the minor (5.3%) reduction in total surface area at 50% flow reduction suggests that little area was dewatered. Rader and Belish (1999) suggested that an increase in water temperature in the dewatered zone in one of their study streams created more favourable conditions for invertebrate growth and development, in turn causing increased densities. This mechanism is an

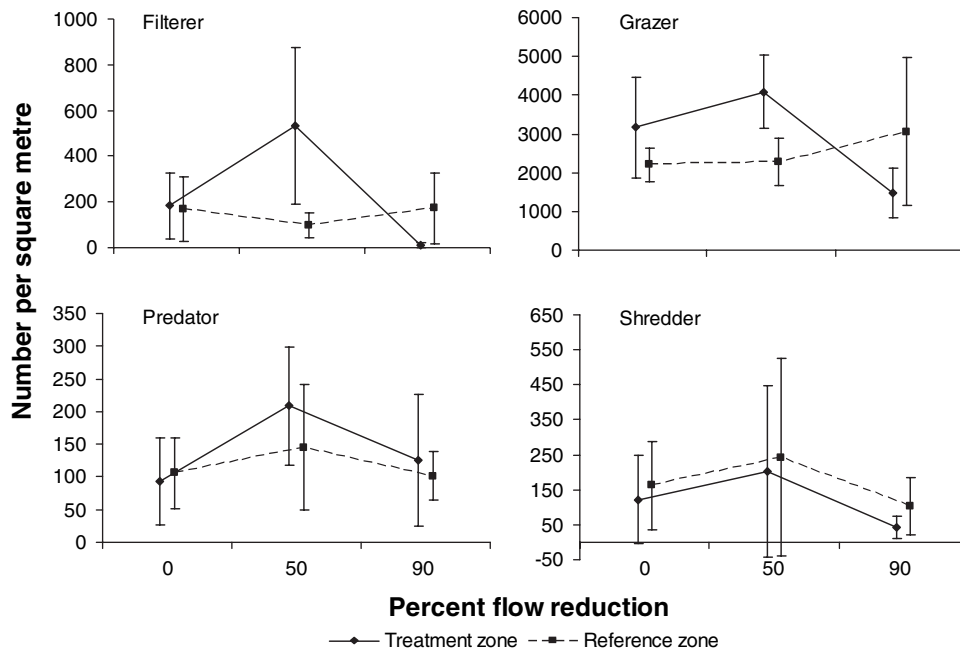


Figure 6. Mean number of insects per square metre (± 2 SE) by functional feeding groups in an experimentally dewatered treatment zone (TZ) and reference zone (RZ) in Hunt Creek. Summer discharge was reduced by 50% in 1994 and 90% in 1997 and 1998. Zero percent flow reduction represents summer discharge before water diversion was initiated in the TZ on June 1 of each year. Summer discharge in the RZ was not altered

unlikely explanation for the findings of our study because Hunt Creek is fed almost entirely by groundwater. Accordingly, average June through August water temperatures collected with an electronic thermometer located 30 m upstream from the dewatered riffle were only 0.3°C warmer during 1993–94 when flow was reduced by 50% as compared to 1997–98 when flow was reduced by 90% (A. J. Nuhfer, MDNR, unpublished data).

As anticipated from the literature (e.g. Bain and Boltz, 1989), Baker and Coon (1995b) noted that although total benthic macroinvertebrate density in Hunt Creek did not decline following a 50% reduction in baseflow in the TZ, the PHABSIM model indicated that reducing stream flow more than 50% would reduce WUA for all taxa and that WUA losses would be substantial. A PHABSIM analysis of brook trout habitat during the same time period that data were collected for this study indicated that brook trout WUA would not be substantially reduced by decreasing stream flow until the discharge declined to nearly $0.09\text{ m}^3/\text{s}$, nearly 20% of summer baseflow (Baker and Coon, 1995a; Nuhfer and Baker, 2004). These results suggest that important brook trout food resources are more vulnerable to dewatering than brook trout foraging or resting habitat (Baker and Coon, 1995b), since brook trout are pool-oriented and therefore less sensitive to flow reduction (Kraft, 1972). Reducing flow by 90% caused insect density in the TZ to drop below that in the RZ, which coincides with the predicted decrease in WUA for common insect taxa at high levels of dewatering. Such a reduction in food resources has the potential to adversely affect populations of salmonids such as brook trout.

The variation in the abundance of benthic macroinvertebrate taxa, particularly insects, at different levels of flow reduction may be partially explained by the feeding strategies and habitat preferences of the organisms. A large proportion of the insect taxa sampled from Hunt Creek were grazers and habitat generalists that occupied both erosional and depositional habitats, such as Baetidae, Chironomidae, Elmidae adults and larvae, and Ephemerellidae. The contribution of these benthic insect taxa to total insect abundance makes it difficult to confidently relate patterns in the abundance of other functional feeding groups, or habitat specialists, to the levels of flow reduction observed. Nevertheless, some general observations can be made relative to habitat preference. For example, taxa preferring only erosional habitats and generalists classified as using both erosional and depositional habitats decreased in the TZ when 90% of flow was diverted but did not decrease in the RZ. The decrease in taxa

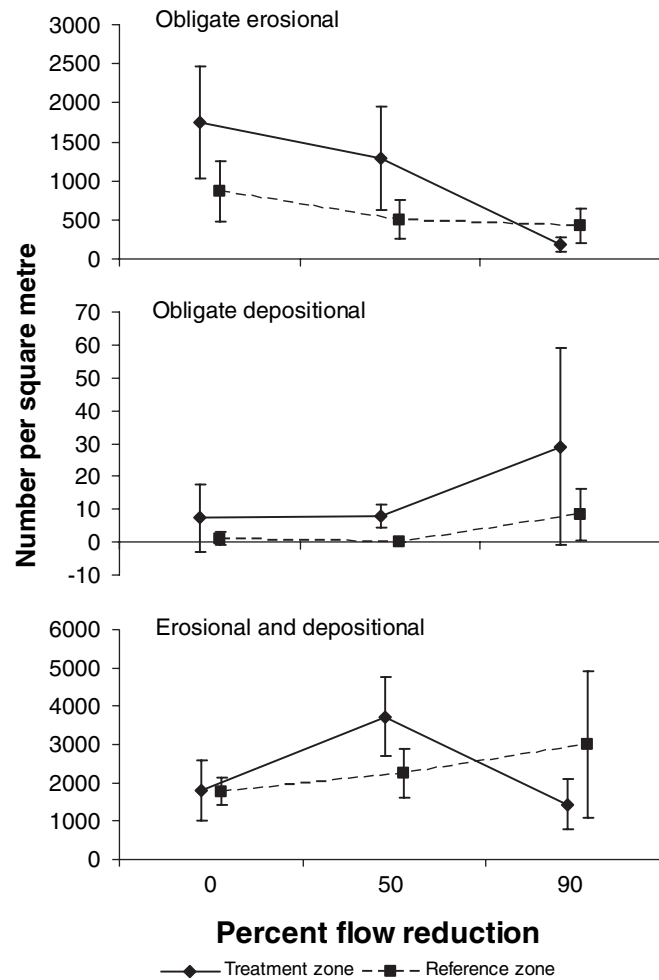


Figure 7. Mean number of insects per square metre (\pm SE) by habitat preference in an experimentally dewatered treatment zone (TZ) and reference zone (RZ) in Hunt Creek. Summer discharge was reduced by 50% in 1994 and 90% in 1997 and 1998. Zero percent flow reduction represents summer discharge before water diversion was initiated in the TZ on June 1 of each year. Summer discharge in the RZ was not altered

Table VII. Statistics for simple linear regression models of the relationship between abundance and WUA for select insect families. N refers to the total number of samples used in the analysis. NS = not significant

Family	N	R ²	F	df	p
Baetidae	15	0.25	4.78	1, 14	0.046
Ceratopogonidae	15	0.09	—	—	NS
Elmidae adult	15	0.22	—	—	NS
Empididae	15	0.26	5.03	1, 14	0.042
Ephemerellidae	15	0.21	—	—	NS
Glossosomatidae	15	0.22	—	—	NS
Heptageniidae	15	0.51	14.62	1, 14	0.002
Hydropsychidae	15	0.22	—	—	NS
Nemouridae	15	0.19	—	—	NS
Perlodidae	15	0.00	—	—	NS
Rhyacophilidae	15	0.07	—	—	NS
Simuliidae	15	0.14	—	—	NS
Tipulidae	15	0.01	—	—	NS

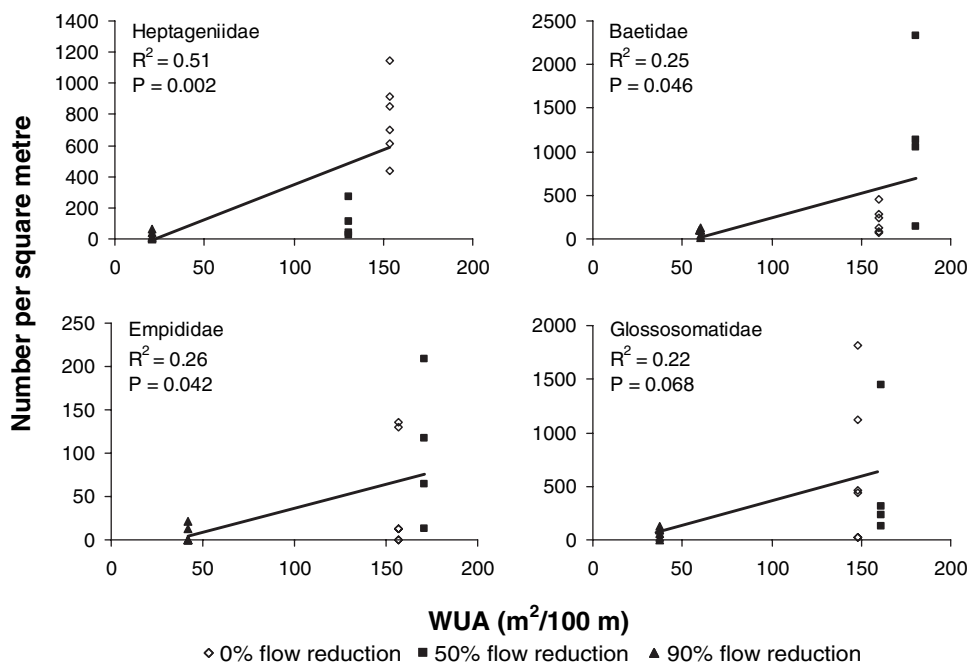


Figure 8. Relation between abundance and weighted usable area (WUA, m²/100 m) for select taxa in an experimentally dewatered treatment zone of Hunt Creek. Diamonds depict abundance during months when summer flow was normal, while squares and triangles show abundance during months when flow was diverted 50% and 90%, respectively

that prefer erosional habitat is likely, since erosional habitats are impacted to a greater extent by flow reduction than depositional habitats (Kraft, 1972). Abundance of obligate depositional zone taxa did not change significantly in either zone, but these taxa were rare in both zones at all levels of flow.

To our knowledge, no other study has compared projections of WUA from a PHABSIM model to observed macroinvertebrate densities to test the assumption of a positive linear relation between WUA and benthic macroinvertebrate abundance. In general, we found that WUA was not linearly related to the density of the majority of the insect taxa modelled and that the relationships between density and WUA were variable, suggesting that the HSC were not reliable or that other factors important in determining benthic insect density were not included in the HSC. Although linear regressions of the density of Heptageniidae and Empididae were significantly related to WUA, their density varied widely at normal flow and at a 50% reduction in flow. The density of obligate erosional taxa and erosional/depositional generalists was usually less variable at the lowest flow tested (90% reduction). Conversely, the density of predators such as Perlodidae and shredders such as Tipulidae was variable at all flows and exhibited no relation to estimates of WUA.

The between-observation variation in insect abundance that occurred when equal percentages of summer flow were diverted indicates that factors other than streamflow volume were affecting population dynamics in Hunt Creek. In addition, patterns of density in the RZ paralleled patterns of density in the TZ in certain cases, suggesting that upstream-downstream effects (i.e. connectivity) or larger-scale environmental or biotic factors contributed to observed trends in abundance rather than reduced flow. Kohler and Wiley (1997) reported that *Glossosoma* populations in many Michigan trout streams, including Hunt Creek, have collapsed due to recurrent pathogen outbreaks. These declines of *Glossosoma* were associated with large increases in periphyton and the abundance of most other grazer and filter-feeder taxa. In Hunt Creek, *Glossosoma* populations in the RZ declined dramatically after 1994 (Kohler and Wiley, 1997). Data collected during our study indicate that a similar decline in *Glossosoma* occurred in the TZ after 1994. Thus, the generally poor relations between WUA and density of various grazer and filter feeding taxa were partially due to the strong effects of the *Glossosoma* population collapse on the overall invertebrate community, a biotic factor that is independent of the reliability of PHABSIM to predict habitat changes.

If the assumption that WUA is positively related to benthic insect abundance is correct, then it is possible that the estimates of WUA from Baker and Coon (1995b) were inaccurate for many of the taxa modelled. Baker and Coon (1995b) made velocity, depth, and substrate measurements at 240 locations distributed across seven transects in the TZ to generate WUA estimates for 13 benthic insect families. However, Railsback (1999) and Kondolf *et al.* (2000) noted that the location and numbers of transects used for habitat sampling exert great influence on WUA predictions. Accordingly, Nuhfer and Baker (2004) used 1 339 locations distributed along 63 transects to generate estimates of WUA for brook trout and found poor correlation between WUA predictions and brook trout abundance and survival rates. They suggested that if their efforts were insufficient to characterize brook trout habitat in the 600 m TZ, then the labour required for accurate projections of WUA would be prohibitive for most resource agencies. Although the extent of the habitat data collected by Nuhfer and Baker (2004) for projecting brook trout WUA was considerably larger than the data used by Baker and Coon (1995b) for benthic invertebrates, we also suggest that the effort required for accurately predicting suitable benthic invertebrate WUA is too labour intensive to be practical. This seems especially true when one considers the lack of consistent relationships between WUA and invertebrate abundance observed in this study.

It is necessary to acknowledge other limitations of our study. Baker and Coon (1995b) recognized that they probably did not adequately sample the first and second instars of many of the taxa in Hunt Creek because of the mesh size used on the Hess sampler, which also applies to our 1997 and 1998 data that were collected using the same protocols. However, Baker and Coon (1995b) suggest that it is unlikely that sampling the early instars would have influenced the results of their study because the direction of predicted changes in WUA (increases or decreases) generally matched the direction of observed changes in the density of insects. Assuming the model predictions are accurate, the same can be said of our 1997 and 1998 data, as the density of most insects did decline at 90% flow reduction as predicted by overall decreases in projected WUA.

We were also unable to compare WUA projections from PHABSIM analysis with the abundance of insect families that occurred in less than 20% or more than 80% of the samples collected by Baker and Coon (1995b), as we used their model predictions rather than constructing our own. Using PHABSIM to predict changes in WUA for infrequently occurring taxa would require a modification of the sampling protocols to more effectively sample those taxa (Baker and Coon, 1995b), as Bovee (1986) noted that HSC constructed for small sample sizes are generally not representative of the habitat suitability requirements of the taxa. Care should also be taken in using PHABSIM to predict the effects of streamflow alterations on frequently occurring taxa. Because most microhabitats are suitable for frequently occurring taxa, HSC for those taxa would be too general to be useful as a predictor of habitat change (Bain and Boltz, 1989; Baker and Coon, 1995b).

Another important note is that we lacked replicated observations of benthic macroinvertebrate abundance at baseflow conditions throughout the entire summer season in years before flow reductions were initiated. Thus, we were limited to data collected prior to June 1 to represent baseflow conditions in the TZ. However, we did have data from an unimpaired, upstream control reach (i.e. the RZ) throughout the entire study. This makes the lack of pre-treatment data in the TZ only a minor concern. Also, we had only one season of data available for the 50% flow reduction, and we were unable to test the effect of other intermediate levels of flow reduction, such as a 75% reduction in baseflow, to determine its influence on benthic macroinvertebrate abundance. Hence, our conclusions are limited to moderate and extreme levels of flow reduction. Finally, a withdrawal of 50% of summer baseflow may have a more negative effect on the benthic macroinvertebrate community in marginal streams that do not have high-quality thermal and physical habitat under summer baseflow conditions.

MANAGEMENT IMPLICATIONS

Resource managers should consider the potential consequences of water withdrawals to all components of the aquatic community including benthic macroinvertebrates because such organisms are indicators of ecosystem health and an important link in food webs. The results presented in this study demonstrated that flow reductions can reduce the density of many benthic insect species, particularly filter feeding and grazing taxa, and those taxa that typically use erosional habitats.

The results of this study are distinctive in that the benthic macroinvertebrate sampling occurred immediately downstream of where water was removed, so there were no thermal effects. Nuhfer and Baker (2004) predicted a

substantial increase in the rate of water warming downstream of the water diversion structure when 75% or more of the flow was diverted, which clearly has implications for coldwater stenothermic organisms such as certain benthic macroinvertebrates. More dramatic shifts in the benthic macroinvertebrate community would likely have occurred several kilometers further downstream, due to the increased rate of warming of the stream, but we were unable to sample them because the flow was returned to the river immediately downstream of the treatment zone. Thus, our results may be somewhat unique to Hunt Creek, but they likely apply to small, groundwater-fed streams draining glacial deposits in the Great Lakes region, and especially those where stream temperatures are unaffected by water withdrawal activities.

Managers should carefully consider the utility of the PHABSIM system in groundwater-fed streams such as Hunt Creek, as we found generally insignificant relationships between WUA and benthic macroinvertebrate abundance. We observed a linear relationship between WUA projections from PHABSIM and the abundance of only three of thirteen benthic insect families. Both of these relationships were variable, indicating that WUA alone is not an accurate predictor of insect abundance in a high-quality trout stream.

Further research should be conducted to determine how well PHABSIM performs at different biological scales. For example, even though we found poor correlation between WUA projections and the density of individual taxa in our study, PHABSIM may still have adequate predictive power for parameters such as biodiversity even if density predictions for individual taxa are poor. Further research is also needed to test the utility of PHABSIM for predicting the response of the benthic macroinvertebrate community to water withdrawals across a wider range of flows, over longer time periods, and in other stream types where habitat conditions (e.g. temperature) may be affected by flow reductions to a greater extent than we observed Hunt Creek. Until this occurs, the PHABSIM technique should be applied with caution in groundwater-fed streams in glaciated areas of the Midwestern United States.

ACKNOWLEDGEMENTS

This study would not have been possible without the efforts of numerous field personnel who assisted in data collection and processing. Current MDNR Fisheries Research technician T. Adams and former technician T. Smigielski assisted with field sampling. B. Sparks-Jackson, D. Simpkins, K. Meyer and J. Anicka provided valuable assistance in the field and laboratory. W. Green assisted in data summarization. Dr. D. Hayes of Michigan State University provided statistical consultation. A. Sutton provided assistance with graphics and figures. J. Mistak, J. Schneider, Dr. R. Vadas, Jr., and an anonymous reviewer provided helpful comments on an earlier version of this manuscript. This research was supported with funds from the Federal Aid in Sport Fish Restoration Act (Study 736, Project F-80-R, Michigan), MDNR Fisheries Division.

REFERENCES

- Alexander GR, Gowing H. 1976. Relationships between diet and growth in rainbow trout (*Salmo gairdneri*), brook trout (*Salvelinus fontinalis*), and brown trout (*Salmo trutta*). *Michigan Department of Natural Resources Fisheries Research Report* **1841**: Ann Arbor.
- Alexander GR, Hansen EA. 1986. Sand bed load in a brook trout stream. *North American Journal of Fisheries Management* **6**: 9–23.
- Allan JD. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 184–192.
- Anderson RO. 1959. A modified flotation technique for sorting bottom fauna samples. *Limnology and Oceanography* **4**: 198–206.
- Armour CL, Taylor JG. 1991. Evaluation of the instream flow incremental methodology by U.S. Fish and Wildlife Service field users. *Fisheries* **16**(5): 36–43.
- Bain MB, Boltz JM. 1989. Regulated streamflow and warmwater stream fish: a general hypothesis and research agenda. U.S. Fish and Wildlife Service Biological Report **89**(18).
- Baker EA, Coon TG. 1995a. Comparison of predicted habitat change and brook trout population response to a simulated irrigation withdrawal in Hunt Creek, Michigan. *Michigan Department of Natural Resources Fisheries Research Report* **2018**: Ann Arbor.
- Baker EA, Coon TG. 1995b. Comparison of predicted habitat change and benthic macroinvertebrate response to a simulated irrigation withdrawal in Hunt Creek, Michigan. *Michigan Department of Natural Resources Fisheries Research Report* **2019**: Ann Arbor.
- Bechara JS, Moreau G, Planas D. 1992. Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 2093–2103.

- Boulton AJ, Lake PS. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* **73**: 2192–2207.
- Bovee KD. 1985. Evaluation of the effects of hydropeaking on aquatic macroinvertebrates using PHABSIM. In *Proceedings of the symposium of small hydropower and fisheries*, Olson FW, White RG, Hamre RH (eds). American Fisheries Society: Bethesda; 236–241.
- Bovee KD. 1986. Development and evaluation of habitat suitability criteria for use in the Instream Flow Incremental Methodology. Instream Flow Information Paper 21. *U. S. Fish and Wildlife Service Biological Report* **86**(7).
- Bovee KD, Newcomb TJ, Coon TG. 1994. Relations between habitat variability and population dynamics of bass in the Huron River, Michigan. *National Biological Survey Biological Report* **1994**(21).
- Castella E, Bickerton M, Armitage PD, Petts GE. 1995. The effects of water abstraction on invertebrate communities in UK streams. *Hydrobiologia* **308**: 167–182.
- Chapman DW. 1966. Food and space as regulators of salmonid populations in streams. *The American Naturalist* **100**(913): 345–357.
- Cobb DG, Galloway TD, Flannagan JF. 1992. Effects of discharge and substrate stability on density and species composition of stream insects. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 1788–1795.
- Dorr JA Jr., Eschman DF. 1970. *Geology of Michigan*. The University of Michigan Press: Ann Arbor.
- Dudgeon D. 1992. Effects of water transfer on aquatic insects in a stream in Hong Kong. *Regulated Rivers: Research and Management* **7**: 369–377.
- Elliott JM. 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *Oecologia* **12**: 329–347.
- Gore JA. 1989. Models for predicting benthic macroinvertebrate habitat suitability under regulated flows. In *Alternatives in Regulated River Management*, Gore JA, Petts DA (eds). CRC Press: Boca Raton; 253–265.
- Gore JA, Judy RD Jr. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1363–1370.
- Gore JA, Layzer JB, Mead J. 2001. Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regulated Rivers: Research and Management* **17**: 527–542.
- Gowan C. 1984. The impacts of irrigation withdrawals on brown trout (*Salmo trutta*) and two species of benthic macroinvertebrates in a typical southern Michigan stream. Master's thesis, Michigan State University: East Lansing.
- Hilsenhoff WL. 1995. Aquatic insects of Wisconsin: keys to Wisconsin genera and notes on biology, habitat, distribution, and species. *Publication No. 3 of the Natural History Museums Council*, University of Wisconsin: Madison.
- Imbert JB, Perry JA. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* **436**: 191–208.
- Kohler SL, Wiley MJ. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* **78**: 2164–2176.
- Kondolf FM, Larsen EW, Williams JG. 2000. Measuring and modeling the hydraulic environment for assessing instream flows. *North American Journal of Fisheries Management* **20**: 1016–1028.
- Kraft ME. 1972. Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada* **29**: 1405–1411.
- Mathur D, Bason WH, Purdy EJ Jr, Silver CA. 1985. A critique of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 825–831.
- McClay W. 1968. Effects of controlled flow reductions on aquatic insects in a stream riffle. Master's thesis, Montana State University: Bozeman.
- Merritt RW, Cummins KW. 1996. *An Introduction to the Aquatic Insects of North America*, (third edition). Kendall/Hunt Publishing Company: Dubuque.
- Milhous RT, Updike MA, Schneider DM. 1989. PHABSIM reference manual: version 2. U.S. Fish and Wildlife Service FWS/OBS 89/16. (Instream Flow Information Paper 26).
- Minshall GW, Winger PV. 1968. The effect of reduction in streamflow on invertebrate drift. *Ecology* **49**: 580–582.
- Morhardt JE. 1986. Instream flow methodologies. Report by EA Engineering, Science and Technology, to the Electric Power Research Institute Research Project 2194-2, Palo Alto, California.
- Nielsen JL. 1992. Microhabitat specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society* **121**: 617–634.
- Nuhfer AJ, Baker EA. 2004. A field validation of the Instream Flow Incremental Methodology (IFIM) in a Michigan brook trout stream. *Michigan Department of Natural Resources Fisheries Research Report* **2068**: Ann Arbor.
- O'Keefe JH, DeMoor FC. 1988. Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers: Research and Management* **2**: 39–55.
- Orth DJ, Maughan OE. 1983. Microhabitat preferences of benthic fauna in a woodland stream. *Hydrobiologia* **106**: 157–168.
- Pennak RW. 1989. *Freshwater Invertebrates of the United States Protozoa to Mollusca*, (third edition). John Wiley and Sons, Inc.: New York.
- Rader RB, Belish TA. 1999. Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management* **15**: 353–363.
- Railsback S. 1999. Reducing uncertainties in instream flow studies. *Fisheries* **24**(4): 24–26.
- Reiser DW, Wesche TA, Estes C. 1989. Status of instream flow legislation and practices in North America. *Fisheries* **14**(2): 22–29.
- SPSS Inc. 2002. *SPSS Base User's Guide 11.5*. SPSS Inc.: Chicago.
- USDA (United States Department of Agriculture). 1999. *1997 Census of Agriculture, Michigan State and County Data, Volume I, Geographic Area Series Part 22*. Document AC97A–22.
- Zorn TG, Seelbach PW. 1995. The relation between habitat availability and the short-term carrying capacity of a stream reach for smallmouth bass. *North American Journal of Fisheries Management* **15**: 773–783.